Journal of Experimental Botany, Vol. 49, Special Issue, pp. 453–460, March 1998

Journal of Experimental Botany

Stomatal conductance predicts yields in irrigated Pima cotton and bread wheat grown at high temperatures

Zhenmin Lu[1], Richard G. Percy[2], Calvin O. Qualset[3] and Eduardo Zeiger[1,4]

[1] Department of Biology, University of California, Los Angeles, Los Angeles, CA 90095–1606, USA
[2] USDA-ARS, Pima Cotton Breeding and Genetics, 37860 W. Smith-Enke Road, Maricopa, AZ 85239, USA
[3] Genetic Resources Conservation Program, University of California, Davis, CA 95616, USA

Received 18 August 1997; Accepted 4 November 1997

Abstract

Recent studies of historical series from Pima cotton and bread wheat bred for higher yields at supra-optimal temperatures under ample water supply have shown that incremental increases in stomatal conductance have accompanied lint and grain yield increases in successive commercial releases. Pima cotton studies showed that the differences in stomatal conductance are under genetic control. F_4 progeny of F_2 plants selected solely for high stomatal conductance had higher lint yields than progeny from low conductance plants. Carbon isotope discrimination is positively correlated with stomatal conductance and yields in both wheat and Pima cotton. A gas exchange study showed that the stomatal response to temperature, but not to light or to water vapour pressure deficit (*VPD*), separated low and high-yielding Pima lines in the same order as their stomatal conductance in field conditions. Selection for higher yields in Pima cotton and bread wheat appear to have generated selection pressures for higher stomatal conductances that are independent of operating pressures for higher photosynthetic rates. The adaptive advantage of higher stomatal conductance appears to be associated with leaf cooling, which provides an avoidance type of heat resistance at supra-optimal temperatures. Lower leaf and canopy temperatures at critical developmental stages associated with flowering and fruiting during July for Pima cotton in Arizona, and February for bread wheat in north-west Mexico appear to favour higher yields. Stomatal conductance could be a valuable selection criterion for higher yields in irrigated crops grown at supra-optimal temperatures.

Key words: Pima cotton, bread wheat, stomatal conductance, high temperature, yield.

Introduction

Stomata play a key role in the acclimation and adaptations of plants to their environment (Zeiger *et al.*, 1987). In agricultural crops, attained yields often lag behind maximal yield potentials because of adverse environmental conditions (Boyer, 1982). Crop physiologists have had limited success in establishing breeding criteria for optimal stomatal performance aimed at increasing environmental fitness and yields (Jones, 1987).

Comparisons of stomatal responses in cultivars with contrasting agronomic properties have been reported (Roark and Quisenberry, 1977; Shimshi and Ephrat, 1975), but no conclusive evidence has emerged on defined relations between stomatal properties and yield. This question can also be addressed in a different way. Breeding programmes with most agricultural crops have successfully increased yields by empirical selection for higher yields, without any explicit selection for yield-related physiological traits. When historical series comprising successive commercial releases are available (Austin *et al.*, 1980), one can ask what, if any, have been the effects of selection on stomatal properties. Banning pleiotropic effects, discrete changes in stomatal properties accompanying yield increases would point to indirect selection pressures on stomatal properties ensuing from selection for higher yields. Elucidation of relationships between any stomatal changes and yield increases would be valuable in the design of strategies for stomatal manipulations aimed at increasing environmental fitness and yields.

Recent studies have used such an approach to investigate the relationship between stomatal conductance and

[4] To whom correspondence should be addressed. Fax: +1 310 825 9433. E-mail: Zeiger@biology.ucla.edu

yields in an historical series of Pima cotton *(Gossypium barbadense*) encompassing 40 years of selection and a nearly 3-fold increase in lint yield. Pilot studies on sorghum, sugarcane and Pima cotton showed the Pima collection to be the most favourable material because of a long, sustained selection for higher yields in hot environments within a common germplasm pool (Feaster and Turcotte; 1984, Turcotte *et al.*, 1992). An initial study in a greenhouse showed increases in both photosynthetic rates and stomatal conductance accompanying the increases in lint yield (Cornish *et al.*, 1991). Follow-up studies under field and laboratory conditions have characterized independent selection processes for higher photosynthetic rates and higher stomatal conductance (Lu *et al.*, 1994; Radin *et al.*, 1994) and have identified the stomatal response to temperature as a key stomatal property altered by selection for higher yields and heat resistance (Lu and Zeiger, 1994). The differences in stomatal conductance between the low and high-yielding Pima lines have been found to be genetically controlled (Percy *et al.*, 1996), and available data indicate that selection for higher stomatal conductance on a segregating F_2 population results in higher lint yields in a F_4 population (Radin *et al.*, 1994). The current understanding of the relationship between stomatal conductance and yields in Pima cotton is reviewed below.

An historical series of bread wheat (*Triticum aestivum)* grown in the Yaqui valley, Mexico was used to investigate whether the conclusions attained in the Pima studies could be extended to other crops. Like Pima cotton, bread wheat in north-west Mexico is grown under irrigation at supra-optimal temperatures. Results presented below show that increases in stomatal conductance have accompanied attained grain yield increases in this historical series of bread wheat. These findings underscore similar selection pressures on higher stomatal conductances ensuing from selection for higher yields in both Pima cotton and bread wheat. Available data further suggest that stomatal conductance could be used as an indirect selection criterion for yield increases.

Stomatal conductance and lint yield in Pima cotton

Figure 1A shows the relationship between lint yield and stomatal conductance in the historical series of Pima cotton. The series, comprising eight successive commercial releases (P32, PS-1 … PS-7, Turcotte *et al.*, 1992; Radin *et al.*, 1994; Percy *et al.*, 1996) was grown in a three-replicate randomized block at Maricopa, Arizona, USA (33.1 °N, 111.9 °W, 358 m above sea level) in 1994 and 1995. Seeding rates, randomized plot design, irrigation, growth conditions, and lint yield measurements have been described previously (Lu *et al.*, 1994; Radin *et al.*, 1994; Percy *et al.*, 1996). Stomatal conductance was measured

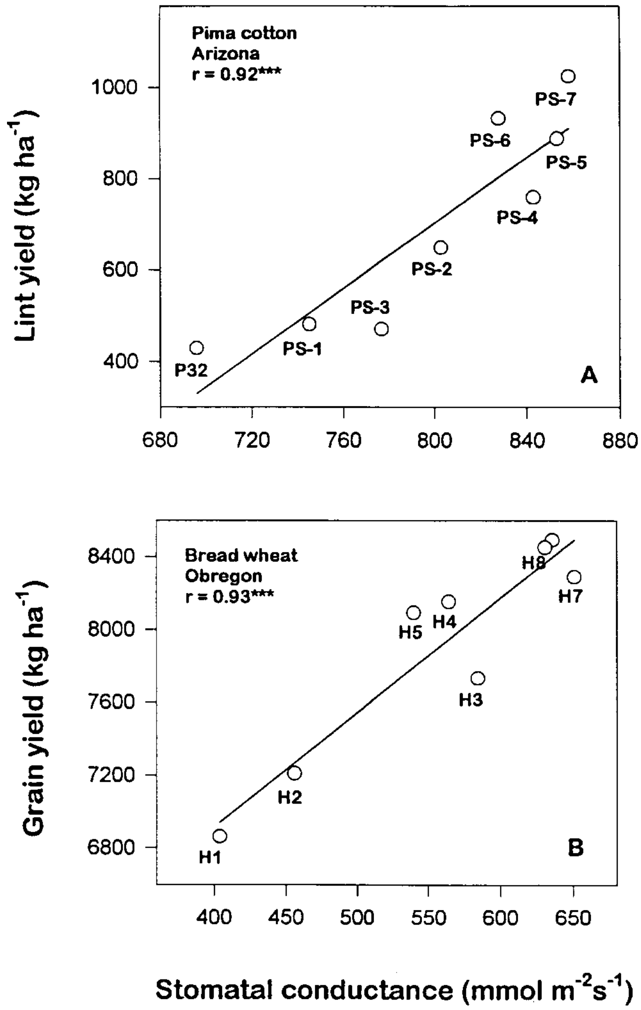

Fig. 1. Relationship between stomatal conductance and yield potential in Pima cotton and bread wheat. (A) Stomatal conductance and lint yield in historical series of Pima cotton measured at Maricopa, AZ. The eight lines were grown in a 3-replicate randomized block in 1994 and 1995. Stomatal conductance from about 35 plants per line were measured each year, data are the average of two years. Lint yields for each line were measured at the end of the season each year, data shown are the average for the two years. (B) Stomatal conductance and grain yield in an historical series of bread wheat measured at Obregon, Mexico. The eight lines were grown in a 3-replicate randomized block in 1993–95. Stomatal conductance from flag leaves of about 30 plants per line was measured during the grain filling stage each year. Grain yields were obtained every year. Data shown are the average for the 3 years. The eight lines (H1 to H8), listed in their order of release, are Pitic, Siete Cerros, Yecora, Nacozari, Ciano, Seri, Oasis, and Super Kauz.

in July, the time of peak flowering and fruiting, as described in Radin *et al.* (1994). Measurements were made between 1 p.m. and 3 p.m., the time at which genotypic differentiation for stomatal conductance is maximal (Lu *et al.*, 1994).

Lint yield in Pima cotton has increased in each subsequent commercial release (Fig. 1A). Stomatal conductance showed a strong, positive correlation with lint yield

($r = 0.92$, $P < 0.001$; Table 1), and increased about 30 mmol m^{-2} s^{-1} per 100 kg ha^{-1} increase in lint yield.

Are selection pressures on higher photosynthetic rates mediating the observed increases in stomatal conductance in Pima cotton?

A steady-state gas exchange study (Lu and Zeiger, 1994) has confirmed previous work in a greenhouse (Cornish *et al*., 1991) showing that photosynthetic rates in Pima lines have increased in parallel with yields. These increases in photosynthetic rates provide a possible explanation for the observed increases in stomatal conductance. Since steady-steady photosynthetic rates are usually tightly coupled to stomatal conductance (Wong *et al*., 1979), applied selection pressures for higher yields could have resulted in an indirect selection for higher photosynthetic rates. The observed higher stomatal conductances would be functionally related to the higher photosynthetic rates, in the absence of any selection pressure on stomatal conductance proper.

Several lines of evidence, however, point to intrinsic selection pressures on higher stomatal conductance in the Pima breeding programme, independent of any operating selection pressures on higher photosynthetic rates. Measurements of photosynthetic rates in the field obtained with a portable steady-state gas-exchange system (PP System, Inc. Haverhill, MA, USA; model CIRAS-1) in the same leaves used for the conductance measurements presented in Fig. 1A, showed variation in photosynthetic rates, with Pima 32 leaves having the lowest, and Pima S-5 the highest rates (16.2 and 19.5 μmol m^{-2} s^{-1}, respectively). There was, however, no significant correlation between photosynthetic rates and lint yield, or between photosynthetic rates and the order in which the lines were commercially released (Table 1).

Segregation for stomatal conductance in an F_2 population of a cross between high and low conductance, Pima parents (Radin *et al*., 1994), resulted in late morning, field conductance values ranging between 0.6 and 1.1 mol m^{-2} s^{-1}. The conductance values had no relation with measured photosynthetic rates, suggesting that photosynthetic capacity and the mechanisms regulating stomatal conductance were segregating independently in the F_2 population. Furthermore, there was no evidence for stomatal limitations to photosynthesis at the conductance values prevailing during the morning. Stomatal conductances measured at mid-afternoon were lower, presumably because of the higher air temperatures and *VPD*, and ranged between 0.1 and 0.8 mol m^{-2} s^{-1}. There was a positive relationship between photosynthetic rate and stomatal conductance in the low range of conductance values, up to about 0.4 mol m^{-2} s^{-1}, but no apparent relation at higher conductance values. These data suggest an upper limit for stomatal limitations to photosynthesis in this F_2 population at around the 0.3–0.4 mol m^{-2} s^{-1} range (Radin *et al*., 1994), and fail to support the hypothesis that the observed variation in stomatal conductance was mediated by variation in photosynthetic rates.

Stable carbon isotope discrimination was positively correlated with stomatal conductance and yields in low and high yielding commercial Pima lines (Lu *et al*., 1996). As discussed in detail in Lu *et al*. (1996), a positive correlation between carbon isotope discrimination and stomatal conductance indicates that the observed increases in stomatal conductance in the Pima series have exceeded the increases in photosynthetic rates, providing further evidence for independent selection pressures on higher stomatal conductance, and for a relationship between stomatal conductance and yield that is independent of photosynthetic rate.

Table 1. *Linear correlation matrix for the data shown in Fig. 1 and Table 2*

	Pima cotton		
	Correlation coefficient		
	Release order	Yield	g_s
Yield	0.94***	–	
g_s	0.83**	0.92***	–
Pn	0.46^{NS}	0.49^{NS}	0.68^{NS}
	Bread wheat (Obregon)		
	Correlation coefficient		
	Release order	Yield	g_s
Yield	0.92***	–	
g_s	0.89**	0.93***	–
Pn	0.25^{NS}	0.02^{NS}	0.08^{NS}
	Bread wheat (Tulelake)		
	Correlation coefficient		
		Yield	g_s
g_s		0.64**	–
Pn		0.18^{NS}	0.66*

*,**,*** Significant at $P < 0.05$, 0.01, and 0.001 probability levels, respectively; NS, not significant at $P < 0.05$ probability level; g_s, stomatal conductance; *Pn*, photosynthetic rate.

Evidence for selection pressures on the stomatal response to temperature in Pima cotton

Exclusion of selection-dependent changes in photosynthetic rates as the primary reason explaining the observed relation between stomatal conductance and lint yield in Pima cotton (Fig. 1A), shifted the research focus to possible selection pressures operating on higher stomatal conductance proper.

Stomatal conductance is an integrated output of many physiological processes in the guard cells (Zeiger *et al.*, 1987), making it unlikely that selection pressures on stomatal conductance *per se* could result in altered gene frequencies and expression determining stable populations with high stomatal conductance. More likely, selection pressures would operate on specific stomatal responses regulated by sensory transduction processes amenable to genetic control. For instance, selection pressures on lower stomatal conductances that provide an adaptive advantage in water-limited environments could favour genotypes expressing higher concentrations of abscisic acid. Under this rationale, the stomatal responses to light, *VPD* and temperature were compared in lines of the Pima historical series, in order to determine whether the observed increases in stomatal conductance could be related to changes in a specific stomatal response (Lu and Zeiger, 1994). There were no differences between low and high yielding Pima lines in their stomatal responses to light or *VPD*. On the other hand, the lines were clearly distinguishable by their stomatal response to temperature, and the ranking of the stomatal conductance values as a function of temperature matched the line ranking for stomatal conductance values in the field, and for lint yield (Lu and Zeiger, 1994). These findings suggest that selection for higher yields and heat resistance has altered the stomatal response to temperature in Pima cotton.

This study also underscored key differences between the temperature responses of photosynthesis and stomatal conductance. In high-yielding lines such as Pima S-6, photosynthetic rates were nearly constant between 24 °C and 36 °C. Stomatal conductance on the other hand, increased linearly with temperature in that temperature range from about 0.55 to about 0.8 mol m^{-2} s^{-1}. Since the increases in stomatal conductance at higher temperatures did not result in higher photosynthetic rates, there was no apparent advantage for higher conductances in the advanced lines in terms of carbon gain (Lu and Zeiger, 1994). These results further suggest that the operating selection pressures on higher stomatal conductance cannot be explained by an adaptive advantage of enhanced carbon gain.

Additional evidence for changes in the stomatal response to temperature in the Pima series was obtained in a growth chamber study of F_2 plants segregating for stomatal conductance. At the lower temperatures used in this study, all F_2 segregants showed similar, relatively low conductances. At higher temperatures, there was a marked phenotypic differentiation among the F_2 segregants, with some plants retaining low conductances, others showing moderate increases and others showing large increases in conductance. The slope of the conductance increases as a function of temperature for each F_2 segregant predicted the measured conductance values at high temperature (Lu *et al.*, 1994). These results indicate that the F_2 population was segregating for the sensitivity of the stomatal response to temperature, and that the stomatal response to temperature was a primary determinant of prevailing conductances. This conclusion is supported by another study showing that isolated guard cells from high conductance, high yielding lines have higher respiration and proton pumping rates as a function of temperature than low conductance, low yielding lines (Srivastava *et al.*, 1995). Taken together, the field and laboratory studies with intact leaves, and the results with isolated guard cells suggest that genetic changes in the high yielding Pima lines have altered guard cell properties controlling the stomatal response to temperature, which result in higher stomatal conductances in the field.

It is significant that in the field, morning conductances were relatively high in all lines (Lu *et al.*, 1994; Radin *et al.*, 1994). Both temperature and *VPD* increased in the afternoon, and the ensuing differences in stomatal conductance between lines resulted from the fact that stomata from the high yielding lines closed *less* than those from the low yielding ones. These responses were qualitatively different from those observed in the controlled environments described above, in which all lines had low conductances at low temperature, and the differences between lines at high temperatures resulted from larger conductance increases in the high yielding lines. *VPD* was kept constant in the controlled experiments, but increased sharply in the field, and incident radiation was substantially higher in the field than in the controlled experiments. Interactions between the light, *VPD* and temperature responses of stomata might underlie the observed differences, which could indicate that the higher temperature sensitivity of the stomata from the high-yielding lines overrides closing signals from the *VPD* response (Grantz *et al.*, 1987), resulting in more pronounced stomatal closing in the low yielding lines.

Adaptive advantage of higher stomatal conductance in Pima cotton

Operating selection pressures for higher stomatal conductances in the Pima breeding programme imply an adaptive advantage of the higher conductances. Besides their important effect on CO_2 uptake, higher stomatal conductances lower leaf temperature, therefore providing a distinct adaptive advantage in hot environments. Optimal daytime temperatures for Pima cotton are below 30 °C (Reddy *et al.*, 1992), while air temperatures in the Pima growing areas of Arizona often exceed 40 °C. Leaf evaporative cooling thus provides an avoidance type of heat resistance that reduces the gap between optimal temperatures and prevailing air temperatures. Leaf-air temperature differences in a heat sensitive landrace, Sea Island, a low yielding commercial line, Pima 32, and a high yielding line, Pima S-6, were about −1 °C, −3 °C and −4.5 °C, respectively (Radin *et al.*, 1994; Lu *et al.*, 1994). A trend towards higher stomatal conductance and lower leaf temperature has persisted in a subsequent commercial release, Pima S-7 (Fig. 1A).

Lower leaf temperatures could also favour higher yields via a reduction in fruit abscission. It is well known to cotton breeders and growers that high temperature periods during the month of July, the time of peak flowering and fruiting, can cause sizeable yield losses because of fruit abscission. A quantitative estimate of such a temperature effect is evident from an analysis of the relationship between maximum day temperatures and lint yields in Pima cotton over an 11-year period (Lu *et al.*, 1997). This analysis showed that July maximal temperatures, but not June or August maxima, had a strong negative correlation with lint yields, with yields decreasing about 110 kg ha^{-1} for each °C increase in maximum day temperature (Lu *et al.*, 1997). Visual inspection of neighbouring plots of the lines from the historical Pima series grown at Maricopa, AZ clearly showed that high temperature periods in July resulted in extensive fruit abscission in the low-yielding lines, but not in the high-yielding lines. If heat stress signals sensed by the leaves are transduced into hormonal processes eliciting fruit abscission, cooler leaves might remain below the threshold temperatures triggering abscission signals.

Selection for higher stomatal conductance can increase lint yields in Pima cotton

Given that selection for higher yields in Pima cotton has resulted in stomatal conductance increases in each successive commercial release, can explicit selection for higher conductance increase yields? This question was addressed in a study of F_2 progeny from a cross between the heat-sensitive, low yielding landrace, St Vincent Sea Island and an elite, high yielding *G. barbadense* line, P70 (Radin *et al.*, 1994). High and low conductance F_2 segregants were identified in the field and their F_3 progeny was grown the following year. Individual F_4 populations, obtained by unselected bulk harvest of individual F_3 progeny rows, were planted a year later. Stomatal conductance and lint yields were determined in the F_3 and F_4 populations (Radin *et al.*, 1994). The genetic control of stomatal conductance was evident from the close relationship between stomatal conductance of the F_4 populations and their F_3 parents (Fig. 2A). There was also a significant, positive relationship between stomatal conductance and lint yields in the F_4 populations (Fig. 2B). These data indicate that stomatal conductance could be used as an indirect selection trait for high yields in irrigated crops grown at supra-optimal temperatures.

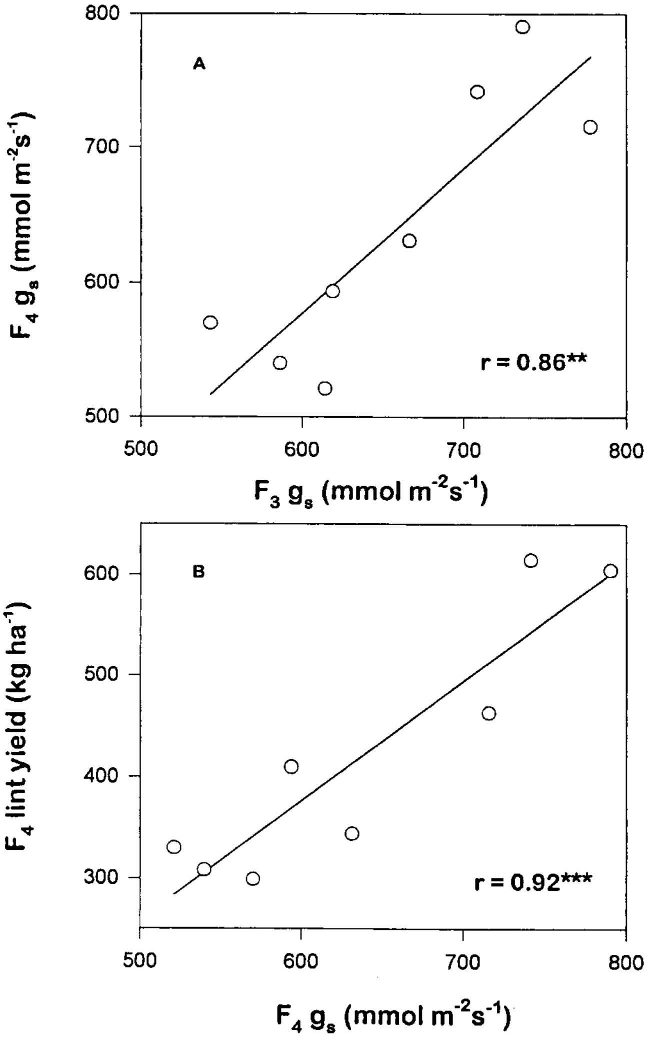

Fig. 2. (A) Close correlation of stomatal conductance in the F_3 and F_4 generations of a cross between a low-yielding, heat-sensitive landrace, St Vincent Sea Island and a high yielding, elite Pima line, P70. (B) Relationship between lint yield and stomatal conductance in F_4 progeny of F_2 plants selected for stomatal conductance. Each point ($n=40$) represents a single F_4 population derived by bulk harvesting individual F_3 populations. Lint yields for each F_4 population were obtained by mechanical harvesting of plots at the end of the season. For detailed methods see Radin *et al.* (1994).

Stomatal conductance and grain yield in bread wheat

The observed increases in stomatal conductance as a function of yield in Pima cotton posed the question of whether a similar relation could be found in other crops grown under irrigation at supra-optimal temperatures. Crop physiologists at the International Maize and Wheat Improvement Center (CIMMYT) have measured lower canopy temperatures as a function of yields in an historical series of eight semi-dwarf bread wheat varieties released by CIMMYT between 1962 and 1988 (Rees *et al.*, 1993). This series has been grown yearly near Cd. Obregon, Sonora, Mexico, for yield potential assays under optimal irrigation and fertilization conditions (Sayre *et al.*, 1997). The lower canopy temperatures suggested to us that the bread wheat series could show increases in stomatal conductances associated with yields similar to those documented for Pima cotton. Stomatal conductance and photosynthetic rates from flag leaves were measured in February in three consecutive years (1993–95) with a Li-Cor 1600 steady-state porometer and an ADC portable gas exchange system, respectively (Rees *et al.*, 1993). The relationship between grain yield and stomatal conductance in the historical series of bread wheat is shown in Fig. 1B. Similar to the findings with Pima cotton, stomatal conductance and yields were highly correlated ($r = 0.93$, $P < 0.001$).

Stomatal conductance, photosynthetic rates and yields were also measured at around anthesis time in a collection of 13 old and recent varieties representing a broad range of yield potentials and tolerance to environmental stress, in spring-planted trials in Tulelake, California, USA in 1995. There was significant variation in all three parameters (Table 2) and yields were positively correlated with stomatal conductance but not with photosynthetic rates (Table 1). Measurements of stomatal conductance in 1996 showed similar results (not shown), and the correlation for two-year mean yield and stomatal conductance was 0.58 ($P < 0.01$).

The remarkable similarity in the relationship between stomatal conductance and yield in the historical series of Pima cotton and wheat supports the hypothesis that selection pressures for higher yields in irrigated crops grown at supra-optimal temperatures generate strong indirect pressures for higher stomatal conductance. A possible relation between photosynthetic capacity and yield has been extensively studied in wheat (Evans, 1993) and it could be the underlying cause of the positive relation between stomatal conductance and yield (Fig. 1B, Table 2). However, as argued above for Pima cotton, several lines of evidence suggest that this is not the case. Photosynthetic rates were not significantly correlated with yield in the CIMMYT historical series (Table 1) nor in the varieties studied at Tulelake (Table 2). Furthermore, grain yields were not significantly correlated with chlorophyll content or biomass in the CIMMYT historical series (Rees *et al.*, 1993). If the highly significant correlation between stomatal conductance and yields (Fig. 1B; Table 2), would be a consequence of a positive relationship between high photosynthetic rates and yields, one would expect that such a relationship could be empirically demonstrated. This was not the case. The genetic basis for variation in stomatal conductance of wheat has not yet been established, but initial evidence suggests that the variation is controlled by independent or linked genes, rather than pleiotrophy.

A study of carbon isotope discrimination in bread wheat has shown a positive correlation between stomatal conductance and yield (Condon *et al.*, 1990). As discussed above in connection with similar results obtained with Pima cotton, such a relation indicates that stomatal conductance has increased relatively more than photosynthetic rates in high yielding lines.

It should be noted that planting density in Pima cotton has been increased dramatically in recent years. The Pima breeding programme has achieved large changes in plant architecture and substantial decreases in leaf size (Lu *et al.*, 1994), and both trends have facilitated increases in plant density. Bread wheat is grown in solid stands. Denser canopies tighten the coupling between leaf and canopy temperature (Lu *et al.*, 1994) and should thus enhance adaptive advantages of higher stomatal conductances associated with lower leaf temperature.

Conclusions

Extant strategies aimed at altering stomatal properties in breeding programmes seeking increased yields have

Table 2. *Post-anthesis stomatal conductance, photosynthetic rates and grain yields of bread wheat varieties grown at Tulelake, California in 1995*

Varieties	Grain yield (kg ha^{-1})	Stomatal conductance (mmol m^{-2} s^{-1})	Photosynthetic rate (μmol m^{-2} s^{-1})
KLM4-3B	2890 g	356 fg	11.3 abcd[a]
KLM4-1B	4490 f	261 h	11.5 abcd
Hahn2/PRL	6860 e	461 bcd	12.7 ab
Cruz Alta	7170 e	397 def	10.7 bcd
Galvez	7420 e	360 f	9.8 d
KRL 1-4	8200 d	433 cde	11.0 abcd
Anza	8380 d	433 cde	12.0 abc
Sakha	8380 d	293 gh	10.0 cd
Serra	8700 cd	440 cde	11.2 abcd
Pavon 76	9050 c	383 ef	11.5 abcd
Perula	9080 c	521 ab	13.0 a
Kauz	9700 b	490 abc	11.3 abcd
Seri 82	10340 a	550 a	12.7 ab

[a]Means in the same column followed by the same letter are not significantly different at $P < 0.05$ level.

usually attempted to decrease stomatal conductance in order to improve water use efficiency (Jones, 1987). Within that perspective, the remarkable increases in stomatal conductance associated with higher yield potential in both Pima cotton and bread wheat are unexpected. Furthermore, many studies have shown that attained yield advances in most agricultural crops have resulted from a higher harvest index, rather than from higher photosynthetic rates (Evans, 1993). In the absence of selection pressures for higher photosynthetic rates, higher stomatal conductances could be disadvantageous because of wasteful water use.

Available data indicate that the observed increases in stomatal conductance underlie an adaptive advantage not directly related to photosynthesis. Higher stomatal conductance lowers leaf and canopy temperature and thus appears to provide an avoidance type of heat resistance to irrigated crops grown at supra-optimal temperatures. If correct, this hypothesis predicts that Pima cotton selected for higher yields under milder temperatures such as those prevailing in the San Joaquin Valley in California, or bread wheat bred for higher yields in Sweden, would not show increases in stomatal conductance associated with higher yields, because of the absence of an adaptive advantage of lower leaf temperatures. Direct tests of this hypothesis assessing the effect of leaf temperature on yields in temperature-controlled environments would also be valuable, although more demanding because of a need to control temperature in environments sufficiently large to also measure yields.

The Pima studies have also shown that, despite the strong environmental dependence of stomatal conductance, existing genetic variation can be successfully manipulated to produce stable populations with contrasting conductance levels. Available evidence suggests that the selection pressures on enhanced leaf cooling was exerted, at least in part, via genetic changes in sensory transducing processes associated with the stomatal response to temperature.

The increases in lint yield observed in F_4 progeny from F_2 segregants selected solely for stomatal conductance indicate that stomatal conductance could be used as an indirect selection criterion for higher yields in irrigated crops grown at supra-optimal temperatures. Further selection studies could offer a conclusive test for the hypothesis that selection pressures on higher stomatal conductance are independent of changes in photosynthetic properties. Since stomatal conductance and photosynthetic capacity appear to segregate independently in F_2 populations segregating for both traits (Radin *et al.*, 1994), higher yields achieved by selection for high stomatal conductance need not be coupled to concomitant higher photosynthetic rates. If selection for stomatal conductance during several generations can stabilize high yield, high conductance populations with varying photosynthetic rates, such results would demonstrate a stomatal conductance–yield relationship independent of photosynthesis. Ongoing work on molecular markers for stomatal conductance and yield in wheat and cotton, and on the feasibility to introgress genes for high stomatal conductance in order to increase yields, should provide further insight on the relationship between stomatal conductance and crop productivity.

Acknowledgements

Research supported by grants from the Department of Agriculture 91–03070 and the Department of Energy of the United States DE-FG03–93ER61688. We thank Dr K Sayre and the Crop Management and Physiology Group at CIMMYT for their support.

References

Austin RB, Binham J, Blackwell RD, Evans LT, Ford MA, Morgan CL, Taylor M. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *Journal of Agricultural Science* (Cambridge) **94,** 675–89.

Boyer JS. 1982. Plant productivity and environment. *Science* **218,** 443–8.

Condon AG, Farquhar GD, Richards RA. 1990. Genotypic variation in carbon isotope discrimination and transpiration efficiency in wheat. Leaf gas exchange and whole plant studies. *Australian Journal of Plant Physiology* **17,** 9–22.

Cornish K, Radin JW, Turcotte EL, Lu ZM, Zeiger E. 1991. Enhanced photosynthesis and stomatal conductance of Pima cotton (*Gossypium barbadense* L.) bred for increased yield. *Plant Physiology* **97,** 484–9.

Evans LT. 1993. *Crop evolution, adaptation and yield*. Cambridge University Press.

Feaster CV, Turcotte EL. 1984. Registration of Pima S-6 cotton. *Crop Science* **24,** 322.

Grantz DA, Moore PH, Zeiger E. 1987. Stomatal responses to light and humidity in sugarcane: prediction of daily time courses and identification of potential selection criteria. *Plant, Cell and Environment* **10,** 197–204.

Jones HG. 1987. Breeding for stomatal characters In: Zeiger E, Farquhar GD, Cowan IR, eds. *Stomatal function*. Stanford University Press, 431–43.

Lu ZM, Chen J, Percy RG, Sharifi MR, Rundel PW, Zeiger E. 1996. Genetic variation in carbon isotope discrimination and its relation to stomatal conductance in Pima cotton (*Gossypium barbadense*). *Australian Journal of Plant Physiology* **23,** 127–32.

Lu ZM, Chen J, Percy, RG, Zeiger E. 1997. Photosynthetic rate, stomatal conductance and leaf area in two cotton species (*Gossypium barbadense* and *Gossypium hirsutum*) and their relation to heat resistance and yield. *Australian Journal of Plant Physiology* **24,** 693–700.

Lu ZM, Radin JW, Turcotte EL, Percy RG, Zeiger E. 1994. High yields in advanced lines of Pima cotton are associated with higher stomatal conductance, reduced leaf area and lower leaf temperature. *Physiologia Plantarum* **92,** 266–72.

Lu ZM, Zeiger E. 1994. Selection for higher yields and heat resistance in Pima cotton has caused genetically determined changes in stomatal conductance. *Physiologia Plantarum* **92,** 273–8.

Percy RG, Lu ZM, Radin JW, Turcotte EL, Zeiger E. 1996. Inheritance of stomatal conductance in Pima cotton (*Gossypium barbadense*). *Physiologia Plantarum* **96,** 389–94.

Radin JW, Lu ZM, Percy RG, Zeiger E. 1994. Genetic variation for stomatal conductance in Pima cotton and its relation to improvements of heat adaptation. *Proceedings of the National Academy of Sciences, USA* **91,** 7217–21.

Reddy KR, Hodges HF, McKinion JM, Wall GW. 1992. Temperature effects on Pima cotton growth and development. *Agronomy Journal* **84,** 237–43.

Rees D, Sayre K, Acevedo E, Nava Sanchez T, Lu ZM, Zeiger E, Limon A. 1993. Canopy temperatures of wheat: relationship with yield and potential as a technique for early generation selection. *Wheat Special Report* **70,** Mexico, D.F: CIMMYT.

Roark B, QuisenberryJE. 1977. Environment and genetic components of stomatal behavior in upland cotton. *Plant Physiology* **59,** 354–6.

Sayre KD, Rajaram S, Fischer RA. 1997. Yield potential progress in short bread wheats in Northwest Mexico. *Crop Science* **37,** 36–42.

Shimshi D, Ephrat J. 1975. Stomatal behavior of wheat cultivars in relation to their transpiration, photosynthesis and yield. *Agronomy Journal* **67,** 326–31.

Srivastava A, Lu ZM, Zeiger E. 1995. Modification of guard cell properties in advanced lines of Pima cotton bred for higher yields and heat resistance. *Plant Science* **108,** 125–31.

Turcotte EL, Percy RG, Feaster CV. 1992. Registration of 'Pima S-7' American Pima cotton. *Crop Science* **32,** 1291.

Wong SC, Cowan IR, Farquhar GD. 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* **282,** 424–6.

Zeiger E, Farquhar G, Cowan I. 1987. *Stomatal function*. Stanford University Press.